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Microbiology and the species problem

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Abstract This paper examines the species problem in microbiology and its implications for the species problem more generally. Given the different meanings of 'species' in microbiology, the use of 'species' in biology is more multifarious and problematic than commonly recognized. So much so, that recent work in microbial systematics casts doubt on the existence of a prokaryote species category in nature. It also casts doubt on the existence of a general species category for all of life (one that includes both prokaryotes and eukaryotes). Prokaryote biology also undermines recent attempts to save the species category, such as the suggestion that species are metapopulation lineages and the idea that 'species' is a family resemblance concept.

Keywords Microbiology · Prokaryotes · Species · Species category · Species concepts

Introduction

The species problem is the problem of determining the correct theoretical definition of 'species.' As anyone familiar with the literature on species knows, there is no consensus on the proper definition of 'species' (Ereshefsky 1992a; Wilson 1999). There is not even a consensus on whether a species category exists in nature. General discussions of the species problem tend to focus on species concepts that were designed with eukaryotes in mind. Yet most of life is prokaryotic, and prokaryotes differ significantly from eukaryotes. General discussions of the species problem should pay closer attention to the literature on microbial systematics. Not

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only because most of life is prokaryotic, but also because the species problem becomes even more challenging given the nature of prokaryotes.

This paper begins with a review of prokaryote species concepts. With that in hand, we turn to the species problem for prokaryotes and ask whether it is reasonable to believe that a prokaryote species category exists in nature. As we shall see, current work in microbiology suggests that there is no natural prokaryote species category. Microbiologists are divided on what to do given this result. Some remain optimistic and push for further research that they believe will offer a realistic species concept for prokaryotes (Dykuizen and Green 1991; Lan and Reeves 2001; Cohan 2002). Others are more pessimistic and adopt a nominalistic definition of ‘species’ (Rosselló-Mora and Amann 2001; Stackebrandt 2006). Still other microbiologists suggest that we abandon the search for a prokaryote definition of ‘species’ and start thinking in terms of other kinds of units of evolution (Bapteste and Boucher 2009; Doolittle and Zhaxybayeva 2009). All three answers to the species problem for prokaryotes will be discussed.

If pessimists concerning a natural prokaryote species category are right, and I think they are, then we have reason to be pessimistic about there being a natural species category for all of life (one that includes both prokaryotes and eukaryotes). After all, most of life is prokaryotic. In addition, microbial systematics casts doubt on recent attempts to save the species category. Given the nature of prokaryotes, the idea that there is a common species phenomenon (Brigandt 2003; Griffiths 2006) does not save the species category, nor does the suggestion that ‘species’ is a family resemblance concept (Pigliucci 2003; Wilson et al. 2009). And the idea that species are metapopulation lineages (de Queiroz 2005; Achtman and Wagner 2008) does not rescue the species category either. In short, the thesis of this paper is that given the different meanings of ‘species’ in microbiology, the use of ‘species’ in biology is more multifarious and problematic than commonly recognized.

Prokaryote species concepts

Current approaches to prokaryote species fall into four groups: recombination, ecological, phylogenetic, and nominalist. Let’s consider each in turn. Following the lead of the Biological Species Concept (Mayr 1970), Dykuizen and Green (1991: 7266) suggest that just as eukaryotes form gene pools so do prokaryotes. Citing evidence of recombination among *E. coli*, Dykuizen and Green argue that a viable prokaryote species concept should focus on groups of microbes whose genomes can recombine. Others have taken up this suggestion (Fraser et al. 2007) and are investigating to what extent recombination among strains of bacteria causes those strains to form stable gene pools.

The recombination species concept for prokaryotes departs significantly from the Biological Species Concept (BSC). The BSC and related reproductive concepts assert that species are relatively closed gene pools. The reproductive mechanisms of such species promote successful gene exchange within a species and prevent it across species. Prokaryote reproduction is not sexual but occurs by binary fission or vegetative means. Some prokaryotes successfully exchange and recombine homologous genes. However, groups of prokaryotes that exchange and recombine homologous genes are far from closed gene pools. Prokaryotes exchange homologous and non-homologous genes via *lateral gene transfer*. Such exchange occurs through several processes: transformation (genetic material absorbed by a host), conjugation (cell to cell transfer), and transduction (viral transfer) (Paul 1999). Lateral gene transfer among prokaryotes is not hindered by the sorts of reproductive barriers frequently cited by supporters of the BSC, such as pre- and post-zygotic isolating mechanisms. In fact, the machinery underlying lateral gene transfer works to violate rather than preserve group boundaries (Doolittle and Papke 2006). Consequently, prokaryotes in different taxa frequently exchange non-homologous genes. This even occurs among such distantly related taxa as families and kingdoms (Xu 2004: 777; Gogarten and Townsend 2005: 684). So though some microbes exchange and recombine homologous genes, microbes lack the reproductive barriers that prevent the exchange of non-homologous genes. Thus, microbial species are relatively open gene pools when compared to BSC species.

Another difference between BSC species and microbial species is that eukaryote recombination is whole-genome, whereas prokaryote recombination is usually limited to parts of a genome. Suppose A and B are two distinct microbial species according to the recombination concept. Genetic information from species A is then transferred through lateral gene transfer to the genomes of some organisms in species B. Some parts of the resultant genomes can successfully recombine with members of A, and other parts can successfully recombine with members of B. According to Nesbø et al. (2006) and Lawrence (2002), the question of which recombination species these resultant organisms belong to depends on which part of the genome one chooses. Because different parts of their genome can successfully recombine with different genomes, “different parts of a genome can belong to different biological species, if our species concept is based on the ability to share information though homologous recombination” (Nesbø et al. 2006: 768). Nesbø et al. report that such “chimerism” occurs in the genus Thermotogales, and they suggest that “such chimerism might be the rule, and not the exception, in many prokaryote groups” (ibid.). The occurrence of partial-genome recombination shows that the recombination approach to prokaryotes species is markedly different than the BSC.[1]

A different microbial species concept is Cohan’s ecological concept. Cohan (2002: 467) suggests that “A species in the bacterial world may be understood as an evolutionary lineage bound by ecotype-periodic selection.” According to this concept, bacteria form species that are adapted to specific environments. Periodic selection maintains the coherence of such species by eliminating diversity in a species that arises by mutation and deviates from a species’ niche-specific adaptations. As the environment changes so too will the species. As mutations give rise to more adaptive phenotypes, those genes go to fixation, and less adaptive traits are purged in periodic selection sweeps. An important assumption of the ecological

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[1] A third difference between BSC species and microbial species is that for most eukaryotes recombination is obligatory while it is not for any prokaryotes. (Thanks to an anonymous referee for pointing this out.)

approach is that periodic selection is the primary process responsible for species cohesiveness.

Some have argued that this assumption is mistaken (Fraser et al. 2007: 480). As we have seen, recombination can contribute to the existence of stable gene pools. Such recombination can potentially withstand the periodic selection sweeps that Cohan highlights. But more interestingly, both periodic selection and recombination can act on the same group of organisms such that the recombination species concept and the ecological species concept cross-classify those organisms. Nesbø et al. (2006: 767–768) report that in the genus Thermotoga, some groups of organisms form single species according to the recombination approach but multiple species according to the ecological approach. The recombination and the ecological concepts are offered as monistic approaches to species: a given organism belongs to one and only one species taxon. Yet empirical evidence indicates that a single group of prokaryotes can belong to two different species, though species of different types.

A third approach to prokaryote species uses genetic data to determine phylogenetic relations. Like the general Phylogenetic Species Concepts, the assumption is that prokaryote species are clades (Rosselló-Mora and Amann 2001; Stackebrandt 2006). Microbiologists use various types of genetic data for reconstructing microbial phylogenies and recognizing species. These include: 16S rRNA genes; DNA:DNA hybridization; average nucleotide identity (Konstantinidis and Tiedje 2005); and core or house-keeping genes (Rosselló-Mora and Amann 2001; Stackebrandt 2006; Nesbø et al. 2006). I will discuss these below, but first let me make a general observation about constructing microbial phylogenies using genetic data. Given the frequency of lateral gene transfer among prokaryotes, different parts of an organism's genome have different evolutionary histories. Consequently, phylogenetically based classifications for the same group of organisms vary, and that variation depends on which cluster of genes is chosen for phylogenetic analysis. The result is a multiplicity of phylogenetic trees, where each tree reflects the phylogeny of a different cluster of genes (Doolittle and Bapteste 2007; Franklin 2007).

Consider Lan and Reeves (2001) and Wertz et al.'s (2003) suggestion that core genes should be used for identifying microbial species. Core genes control such functions as cell division and metabolic activity. Auxiliary genes, by contrast, are associated with niche use. The assumption is that organisms that acquire new core genes through lateral gene transfer are rarely viable.[2] Whereas organisms that acquire new auxiliary genes through lateral gene transfer are more frequently viable. Lan and Reeves (2001) argue that core genes should be used in determining prokaryote species because they are less likely to be the result of lateral gene transfer and more likely to indicate true phylogeny. Critics of this reasoning argue that on the average core genes constitute approximately 5% of a genome, and this percentage is too low to represent the phylogeny of the entire genome (Doolittle and Bapteste 2007: 2046). This response turns on the idea that among the various gene phylogenies that run through a genome, there is no basis for asserting that a

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[2] Though in some cases the introduction of foreign core genes may be harmless or even beneficial (Ford Doolittle, pers. comm.).

phylogeny of core genes is *the* phylogeny of a genome. But things are a bit messier than that. Core genes from a single genome can have different phylogenies. Wertz et al. (2003: 1244) construct the phylogenetic trees of six different core genes from the same genome. The result is six different phylogenies. Which is *the* correct phylogeny of the genome in question? There's no obvious answer.

Let's consider two other types of genetic data used for identifying microbial species: 16S rRNA genes and DNA:DNA hybridization. The standard threshold for identifying a species using genes for 16S rRNA is a sequence similarity of 97% or greater. When using DNA:DNA rehybridzation, the reassociation value (reflecting DNA similarity) for identifying a species is 70% or higher. These two different ways of identifying species, however, can and do conflict, resulting in conflicting species classifications of the same set of organisms (Rosselló-Mora and Amann 2001: 47, 54; Konstantinidis and Tiedje 2005; Stackebrandt 2006: 35). Why do they conflict? It is commonly thought that genes for 16S rRNA are more conservative than most genes (Stackebrandt 2006: 35). Those that prefer 16S rRNA genes appreciate their stability and ubiquity. Those that prefer DNA:DNA hybridization prefer it because it better correlates with phenotypic similarity. Does one type of genetic data better reflect microbial phylogeny than another? Doolittle and Bapteste (2007) and Franklin (2007) suggest that these varying genetic approaches are not faulty measures of phylogeny; these approaches simply measure the different phylogenies of different parts of a genome. Various phylogenies run through the same group of organisms, and those phylogenies place those organisms into a plurality of phylogenetic species.

Having looked at three approaches to prokaryote species—recombination, ecological, and phylogenetic—can we say which is the correct one? Perhaps the answer to that question turns on what type of lineage[3] a biologist is interested in: lineages due to periodic selection, lineages whose genes successfully recombine, or phylogenetic lineages. Notice that there is a twofold pluralism here. First, one can sort the same organisms into conflicting classifications depending on whether one sorts those organisms according to recombination, selection, or phylogeny.[4] Call this *inter-approach pluralism*. Second, one can sort the same organisms into conflicting classifications when using the same type of empirical parameter. Call this *intra-approach pluralism*. For example, when different parts of the same genome recombine with different genomes, the recombination approach sorts a single group of organisms into conflicting species classifications. Similarly, when different parts of the same genome have different phylogenies, the phylogenetic approach sorts the same group of organisms into conflicting phylogenetic species.

This blooming, buzzing confusion of ways to classify prokaryotes into species has caused some microbiologists to suggest a nominalistic microbial species concept. Stackebrandt, the former editor of the *International Journal of Systematic*

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[3] By 'lineage' I merely mean either a monophyletic or paraphyletic group of organisms.

[4] We have seen examples where the recombination and ecological species concepts divide the same group of organisms into different species. For examples where the recombination and phylogenetic approaches sort organisms into different species, see Touchon et al. (2009). For examples demonstrating the conflict between the phylogenetic and ecological approaches, see Konstantinidis and Tiedje (2005).

Bacteriology writes, “The nonexistence of species as an objective category… has been recognized by microbiologists for over 20 years. Bacteriologists in particular follow guidelines and recommendations to provide stability, reproducibility, and coherence in taxonomy—although in the final analysis, species description is still subjective” (2006: 36–37). Arguably, the most widely accepted species concepts in microbiology are nominalistic and designed to be operational (Rosselló-Mora and Amann 2001: 59; Stackebrandt et al. 2002: 1044; Hanage et al. 2005: 6; Stackebrandt 2006: 38). One such concept is the “phylo-phenetic species concept” of Rosselló-Mora and Amann (2001: 59). A phylo-phenetic species is “a monophyletic and genomically coherent cluster of individual organisms that show a high degree of overall similarity with respect to many independent characteristics, and is diagnosable by a discriminative phenotypic property” (ibid.).

We can see why the phylo-phenetic species concept is considered nominalistic by tracing Rosselló-Mora and Amann’s (2001: 59–60) description of how phylo-phenetic species are identified. First, 16S rRNA genes or some other genetic marker are used to provide a phylogenetic tree for the organisms in question. The resultant tree is based on selected parts of their genomes and ignores other parts. Which parts are used is chosen on pragmatic grounds. The resultant tree suffices for grouping organisms into taxa, but it is insufficient to rank those taxa. Second, DNA:DNA hybridization is employed to identify groups that have “a high degree of genomic similarity” (ibid.: 60). A 70% degree of similarity in hybridization is normally considered the threshold for identifying species taxa. The 70% threshold is adopted because phenotypic and genotypic similarities tend to agree at levels of 70% or higher. There is no deeper theoretical reason. If there is a disagreement between the initial phylogenetic analysis and the 70% hybridization threshold, the 70% threshold is relaxed. Third, a “phenetic analysis of as many characters as possible is employed as a practical means for ranking” (ibid.: 58). At each stage of identifying a phylo-phenetic microbial species, parameters are chosen for pragmatic rather than theoretical considerations (for example, which genes to use for constructing a phylogeny, the 70% hybridization threshold, and the use of phenetic measures). This does not imply that the individual taxa identified by the phylo-phenetic concept are unreal. They are real: the parameters used for identifying those taxa are empirical parameters (genetic markers for phylogeny, levels of DNA:DNA hybridization, and phenotypic traits). What is nominalistic about the phylo-phenetic species concept is the species category. There is no theoretical claim that those parameters for picking out microbial species are *the* correct ones. They are just parameters chosen for pragmatic reasons. Phylo-phenetic species are another type of taxa called ‘species’ by microbiologists, alongside recombination species, ecological species, and phylogenetic species.[5]

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[5] Some readers of this paper have objected to the claim that phylo-phenetic species taxa are real. Though I stand by this claim, it is worth mentioning that none of the arguments in this paper concerning the reality of a prokaryote species category or a general species category depend on this claim. The diversity found among recombination species, ecological species, and phylogenetic species is sufficient for the arguments that follow.

Is there a prokaryote species category in nature?

What should we make of this situation? Should we think there is a real prokaryote species category in nature? There are several ways to answer this question. An optimist about a real prokaryote species category might promote a wait and see attitude. For example, perhaps with more work we'll find that Cohan's ecological approach to prokaryote species does a nice job explaining why microbes form cohesive taxa. I do not think that will be the case for the reasons mentioned earlier, namely because there are other forces besides ecological ones that cause the existence of microbial lineages.[6] Or perhaps there will be a new and successful approach to prokaryote species we do not yet know about. Nevertheless, given what we know now, prokaryotes are affected by a number of different processes (recombination, selection, parent-offspring relations, and lateral gene transfer), and those processes cause parts of the same organisms to belong to different types of lineages called 'species.' As Doolittle and Papke (2006, 116.5) write in reference to microbes and the species problem, "genomics has given us too many processes with too many possible synergistic and antagonistic effects on genome coherence." The problem with the optimist's wait and see strategy is that it ignores our current knowledge of prokaryotes. Given what we know now, we have good reason to be pessimistic about there being a prokaryote species category in nature (see Lawrence and Retchless 2010, this issue). It is this knowledge of prokaryotes that causes Stackebrandt and others to offer nominalistic accounts of the prokaryote species category. Notice that nominalism concerning the prokaryote species category relies on a striking form of pluralism. As we saw earlier, prokaryote species concepts sort organisms into different types of species (inter-approach pluralism): recombination species, ecological species, phylogenetic species, and phylo-phenetic species. In addition, these approaches sort organisms into different species of the same type (intra-approach pluralism). Recall that the recombination approach sorts the same organisms into different species taxa depending on which part of a genome one is tracking. Similarly, the phylogenetic approach sorts the same organisms into different species taxa depending on which part of a genome one is considering.

Given that prokaryotes are sorted into different types of taxa called 'species,' we have good reason to be sceptical of there being a prokaryote species category in nature. If we are to believe that a putative category is a real category in nature, it should meet some minimum threshold. Arguably, such a category should meet three criteria (Ereshefsky 2009). First, most of the entities in that category should share a common feature. Second, that feature should help us understand the nature of the entities in that category. Third, that feature should distinguish most entities in that category from entities in other categories. The first criterion requires that a putative category have predictive value. If no feature occurs in most of the members of a category, then that category has no predictive value. The second criterion requires that a category have explanatory value: it should cite some feature that helps us understand the nature of the entities in that category. The third criterion requires that

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[6] See Fraser et al. (2007) and Morgan and Pitts (2008) for further reasons to be pessimistic about an all-encompassing ecological approach to prokaryote species.

we can in most cases distinguish entities in a category from entities in other categories. Together these criteria place predictive and explanatory requirements on a category. These requirements, taken together, are weaker than essentialism. They do not require that a feature occur in all the members of a category, nor do they require that a feature occur in only the members of a category. All that is required is that a distinctive explanatory feature occurs in most members of a category.

Is there a distinctive explanatory feature that occurs in most groups of prokaryotes called 'species'? Let's go through some candidates. Are most groups of prokaryotes called 'species' held together by periodic selection, as suggested by the ecological approach? Empirical work suggests otherwise (Fraser et al. 2007: 480; Achtman and Wagner 2008: 432–433; Doolittle and Zhaxybayeva 2009: 753). What about the process of recombination: do most groups of prokaryotes called 'species' have genomes that can successfully recombine? Again, empirical results suggest that the answer is no (Gogarten and Townsend 2005, 684; Achtman and Wagner 2008: 435; Doolittle and Zhaxybayeva 2009: 753). What about the phylogenetic approaches? In this cladistic age, the majority of groups of prokaryotes called 'species' by microbiologists meet the cladistic criterion of being monophyletic. So we have a biologically significant property found in most groups of prokaryotes called 'species.' But there is a problem. The property of being a phylogenetic taxon is not distinctive to those taxa called 'species': all higher taxa, genera on up, are phylogenetic groups as well. In the end, then, the class of taxa called 'species' by microbial systematists fails the minimal threshold for being considered a real category in nature—there is no distinctive explanatory feature found in most prokaryote taxa called 'species.' Consequently, we should be pessimistic of the existence of a natural prokaryote species category.

Considerations such as these cause some microbial systematists to adopt a nominalist species concept for prokaryotes (Rosselló-Mora and Amann 2001; Hanage et al. 2005; Stackebrandt 2006). These biologists are sceptical of the existence of a natural prokaryote species category. Nevertheless, they continue classifying prokaryotes in a Linnaean fashion and use the word 'species.' Other microbiologists pessimistic of a prokaryote species category see the use of 'species' fading into the background. For example, Doolittle and Zhaxybayeva (2009: 754) write that eventually "the word 'species'… will disappear from scientific literature." Some microbiologists are working on replacements for the word 'species.' Bapteste and Boucher (2008, 2009) suggest that microbial taxonomy should classify *composite evolutionary units*: integrated associations of lower-level elements replicated and held together by biological mechanisms. Such evolutionary units are composite because they consist of phylogenetically diverse genes. Furthermore, such evolutionary units occur at different levels of organization. Some may be parts of organisms, some may be whole organisms, and others may be microbial communities such as syntropic microbial consortia. Many composite evolutionary units are not species as traditionally conceived, given that their members are not organisms but genes, gene complexes and communities. Bapteste and Boucher (2009) encourage microbiologists to abandon the notion of microbial species and instead investigate composite evolutionary units.

Is there a general species category in nature?

Thus far the discussion has focused on prokaryotes and whether a prokaryote species category exists in nature. As we have seen, information from microbial systematics gives us reason to doubt the existence of a natural prokaryote category. That result is important because most organisms currently and in the history of this planet are microbes (Rosselló-Mora and Amann 2001: 40; O'Malley and Duprè 2007: 157). So most of life does not belong to a species taxon.[7] This result is striking and worth pausing over. But this is not the end of the problems for the species category. As we shall see in this section, the nature of prokaryotes gives us further reason to doubt the existence of a general species category for all of life. And in the next section, we will see that recent attempts to save a general species category run aground the shoals of microbial systematics.

In the previous section we saw that the disunity of the class of prokaryote taxa called 'species' provides reason to doubt the existence of a natural prokaryote species category. Consider now a more inclusive class: all those taxa picked out by species concepts proposed by microbiologists *and* those taxa picked out by general species concepts, such as the Biological Species Concept (Mayr 1970), the Ecological Species Concept (van Valen 1976), and various Phylogenetic Species Concepts (Baum and Donoghue 1995). That class of taxa, I will suggest, is so heterogeneous that we have reason to doubt the existence of a natural species category for all of life. The claim that the Biological Species Concept, the Ecological Species Concept, and various Phylogenetic Species Concepts pick out different types of taxa has been argued elsewhere (Ereshefsky 1992b, 1998, 2001). I won't highlight that disunity here. Instead, I will highlight discrepancies between those general species concepts and the prokaryote species concepts discussed earlier. At first glance it looks like various approaches to prokaryote species and various general species concepts line up nicely. The recombination approach to prokaryotes and the Biological Species Concept seem to capture the same type of phenomena. And the same might be thought of Cohan's ecological approach and the Ecological Species Concept, as well as phylogenetic approaches in microbiology and the general Phylogenetic Species Concepts. However, these concepts do not so nicely line up: general species concepts and prominent prokaryote species concepts pick out different types of taxa.

Consider some differences. Species under the Biological Species Concept are relatively closed gene pools, whereas recombinant prokaryote species are not genetically closed systems because of lateral gene transfer. Another difference: recombination is whole-genome for the Biological Species Concept, whereas it is partial-genome for microbes. Turning to the Ecological Species Concept, that concept highlights constant stabilizing selection as the cause of species coherence, while the ecological approach in microbiology highlights periodic selection. When it comes to the Phylogenetic Species Concepts, species are either monophyletic taxa

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[7] This is not to say that most organisms do not belong to taxa. The claim here is that most organisms do not belong to *species* taxa. Most (or all) organisms may belong to taxa, but there is no natural species category that those taxa belong to. See below and Ereshefsky (1998, 2009) for further discussion.

(Mishler and Brandon 1987) or diagnostically distinct clusters of organisms (Nixon and Wheeler 1990). Information about gene phylogenies is often used to infer phylogenetic relations among organisms and to posit phylogenetic species. The assumption is that for a group of organisms, a significant number of gene trees will overlap so that we can infer an organismic phylogeny. It is recognized that many gene trees will conflict, but some significant concordance among gene trees is expected (Maddison 1997; Coyne and Orr 2004: 463ff.). For prokaryote species, the genetic information used for recognizing species is often specific types of genes rather than a concordance of available gene trees. Recall that 16SrRNA genes, core genes, and house-keeping genes are frequently used for recognizing prokaryote phylogenetic species. Such species are identified using relatively small sets of genes compared to the data sets used for identifying eukaryote species. So unlike eukaryote phylogenetic species, no significant degree of concordance among gene trees is required for recognizing prokaryote phylogenetic species.

Stepping back from these details, here is the point. First, the taxa called ‘species’ by different prokaryote species concepts vary: some lineages are the result of periodic selection, some consist of organisms whose genomes can successfully recombine, some are phylogenetic units, and still others are identified by phylophenetic factors. Second, the taxa identified as ‘species’ by different general species concepts vary: some lineages are held together by interbreeding and reproductive isolation, some are due to stabilizing selection, and others are the result of phylogeny. Third, these two types of species taxa—those identified by prokaryote species concepts and those identified by the general species concepts—vary: some lineages are due to whole-genome recombination, others are due to partial-genome recombination; some lineages are maintained by periodic selection, others are maintained by stabilizing selection; and, some lineages reflect the concordance of a significant number of genes phylogenies, while other lineages reflect the phylogeny of a relatively small number of genes. The discrepancies and disunity among these types of taxa called ‘species’ is overwhelming. The thought that there is a common distinctive explanatory feature among all of these taxa that renders them and only them ‘species’ seems doubtful. So not only do we have reason to doubt the existence of a natural prokaryote species category, we have reason to doubt the existence of a natural species category for all of life.

Recent attempts to save the species category

Biologists and philosophers that discuss the species problem are all too aware of the disunity of the class of taxa called ‘species.’ In the last 10 years a number of defenses of the species category have been offered (Brigandt 2003; de Queiroz 1999, 2005, 2007; Griffiths 2006; Mayden 2002; Pigliucci 2003; Pigliucci and Kaplan 2006; Wilson et al. 2009). Even without considerations from microbial systematics, such attempts to save the species category face difficulties (Ereshefsky 2009). But in light of microbial systematics, such attempts to save the species category are even more problematic.

Brigandt, for example, argues that despite the differences among the types of taxa that biologists call 'species,' "[i]t is fundamental to realize that biologists address something that might be called the 'species phenomenon'" (2003: 1310). According to Brigandt, 'species' is an "investigative-kind concept" that is used to investigate "a certain perceived pattern among organisms" namely the species phenomenon (ibid.). With Brigandt, Griffiths writes that "it is a manifest fact that organisms form species" and "the existence… of species is a phenomenon that stands in need of explanation" (2006: 10–11; also 2007: 655). The idea, then, is that biologists commonly recognize a type of phenomenon, what Brigandt and Griffiths call the "species phenomenon." When biologists propose species concepts they are proposing ways to explain that phenomenon. There is an intuitive appeal to this line of reasoning: only the most ardent skeptic can deny that nature packages organisms into distinct taxa. Thus, Griffiths writes that when it comes to species "the burden of proof is massively on the side of the skeptic" (2006, 11).

I have two concerns with Brigandt and Griffiths' line of reasoning. First, denying the existence of the species category does not imply that organisms do not form taxa. One can deny the existence of the species category and still allow that nature does contain distinct taxa such as *Homo sapiens* and *Canis familiaris* (Ereshefsky 1998, 2009). The manifest fact Griffiths talks of, namely that there are taxa in the world, does not imply that those taxa belong to an existent category called 'species.' Second, given the diverse nature of the taxa microbiologists call 'species,' there is good reason to doubt the existence of a single prokaryote species phenomenon. Recall that the prokaryote taxa called 'species' conform to a number of different parameters: some are recombination groups, some are ecological groups, others are phylogenetic groups, and still others are phylo-phenetic clusters. The processes that such taxa engage in and the patterns they display, their *taxonomic phenomena*, are quite different. As a number of microbial systematists point out, microbiologists disagree on whether prokaryotes fall into "recognizable discrete centers of variation" and what those centers might even be (Doolittle and Papke 2006: 116.5; also Gevers et al. 2005; Stackebrandt 2006). Given the diversity of taxa called 'species' by microbiologists, we have reason to doubt that there is a unified prokaryote species phenomenon. Furthermore, if there is no unified species phenomenon among prokaryotes, there is no unified species phenomenon for all of life, given that most of life is microbial. The disparity among different taxonomic phenomena called 'species' does not end there. Given the significant differences between prokaryote and eukaryote taxa called 'species,' we have further reason to doubt that there a general species phenomenon.

A different attempt to save the species category employs Wittgenstein's notion of family resemblance. Following Hull (1965), Pigliucci and Kaplan (Pigliucci 2003; Pigliucci and Kaplan 2006) suggest that the species problem can be solved if we treat 'species' as a family resemblance concept. As they point out, different general species concepts highlight different properties of species, such as reproductive isolation, phylogenetic relations, and ecological role (Pigliucci and Kaplan 2006: 221). Some species have one of those properties, some have more; but no one of those properties is the defining characteristic of species. Still, many of those properties are found in more than one type of species. According to Pigliucci (2003:

601), "species represent one large cluster of natural entities… with its members connected by a dense series of threads." The suggestion here is not merely that all species taxa belong to a vast disjunction referred to by the word 'species.' That would be too loose of a connection to solve the species problem, because it allows that the taxa called 'species' might only be connected in a trivial sense. Instead, Pigliucci and Kaplan's solution requires that there be, as Pigliucci describes it, some "dense series of threads" connecting the different taxa called 'species.'

A similar assumption is found in Wilson et al.'s (2009) application of Boyd's (1999) Homeostatic Property Cluster Theory to the species problem. For them, the solution to the species problem involves recognizing that the species category is a homeostatic property cluster concept. Their answer to the species problem is similar to Pigliucci and Kaplan's in that it allows that species taxa have a variety of patterns and processes, yet the unity of the species category is found in there being "causally basic features that most *species* share" (Wilson et al. 2009). Both Pigliucci and Kaplan's and Wilson et al.'s solutions to the species problem assume that there are a sufficient number of overlapping features among taxa called 'species' for positing the species category.

How does this assumption hold up in light of prokaryote systematics? Doolittle and Papke (2006) argue that there are too many processes acting on microbes to assert that there is cluster of overlapping features found in most microbial 'species.' Recall that those microbial taxa called 'species' are the result of periodic selection, successful recombination, or phylogeny (though different parts of a genome have different histories). Wilson et al. (2009) write about "the causally basic features that most species share." What are the causally basic features found in most prokaryote taxa called 'species'? Perhaps all such species are phylogenetic units. But that does not distinguish those taxa from other Linnaean taxa. Nor do any number of processes common to most prokaryote taxa called 'species.' Indeed, the difficulties in finding features that distinguish microbial species from microbial varieties or higher taxa cause many bacterial systematists to be skeptical of the species category (Rosselló-Mora and Amann 2001; Stackebrandt 2006). When we turn to prokaryotes and eukaryotes and look for the causally basic feature for taxa called 'species' our task only gets more difficult, given the differences between prokaryotes and eukaryotes. Similar worries apply to Pigliucci and Kaplan's solution to the species problem. What is the "dense series of threads" among different types of prokaryote taxa called 'species'? Even harder to answer: what is the "dense series of threads" that connects prokaryote 'species' and eukaryote 'species'? The nature of prokaryote taxa, and the differences between prokaryotes and eukaryotes, should cause us to be skeptical of the idea that the taxa called 'species' are linked by a "dense series of threads" or share many "causally basic features." To the extent that taxa called 'species' do share casual similarities, those similarities are shared by all taxa, whether they be called 'varieties,' 'species,' or 'genera.' If a theoretical concept is bereft of any distinctive explanatory or predictive power, then we should be skeptical of that concept corresponding to a real category in nature.

Another recent attempt to save the species category is de Queiroz's (1999, 2005, 2007) General Lineage Concept (Mayden 2002 offers a similar suggestion). Despite the differences among species concepts, de Queiroz argues that all prominent species concepts agree that species are “separately evolving metapopulation lineages” (2005: 1263). De Queiroz suggests that this conception of species is the “single, more general, concept of species” that reconciles all other species concepts (2007: 880). According to de Queiroz, the General Lineage Concept provides the necessary criterion for being a species. The properties that other species concepts disagree over, for example, a lineage’s occupying a unique niche or being monophyletic, are contingent properties of species. They are “secondary” properties of species (de Queiroz 2005: 1264). Some microbiologists endorse de Queiroz’s approach to the species problem. Achtman and Wagner (2008) suggest that the General Lineage Concept can solve the species problem for prokaryotes because it recognizes the diversity of prokaryote taxa called ‘species’ but at the same time offers a unifying commonality—they are all metapopulation lineages.

A difficulty with the General Species Concept is how to distinguish species from higher taxa. De Queiroz distinguishes species from higher taxa by asserting that species are single lineages whereas higher taxa are clades of multiple lineages (1999: 50; 2007: 881). What, then, distinguishes a single lineage from a clade with multiple lineages? De Queiroz (2005: 1265; 2007: 882) writes that the General Lineage Concept does not need to cite the secondary properties mentioned in other species concepts to answer this. Yet de Queiroz offers no alternative criteria for determining when a single lineage becomes a branch with multiple lineages. Moreover, the secondary properties of other species concepts are the properties commonly used to make that determination. Therein lies a problem with thinking that the General Lineage Concept solves the species problem. According to the General Lineage Concept, only lineages are species. But to determine what constitutes a lineage we must turn to other species concepts, and in doing so the heterogeneity of the species category rears its head again. Suppose we want to determine whether there is one metapopulation lineage (a species) or multiple metapopulation lineages (a higher taxon) in a given situation. If the genomes among a group of organisms can recombine but that group consists of multiple ecotypes, there is one species according to the recombination concept but multiple species according to the ecological concept. Or suppose a peripheral isolate buds off a pre-existing lineage and the organisms in that isolate form an ecotype distinct from the ecotype of the organisms in the original lineage. On the ecological concept, the original lineage and its unchanged descendents remain one lineage. On a phylogenetic approach, there are two new lineages (otherwise a paraphyletic ancestral lineage will be posited). In brief, the General Species Concept attempts to solve the species problem by suggesting that only lineages are species. Yet that suggestion does not solve the species problem but merely masks the heterogeneity of the species category, because what constitutes a lineage has multiple answers and those answers vary according to which species concept one chooses.

Back to the future

If the arguments in this paper are sound, then we have good reason to doubt the existence of a prokaryote species category in nature. Similarly, we have good reason to doubt the existence of a general species category for all of life. Nevertheless, one might wonder if a eukaryote species category remains intact (Elliott Sober, pers. comm.). Elsewhere I have argued that there are sufficient discrepancies among interbreeding, ecological and phylogenetic species of sexual eukaryotes to doubt the existence of a natural eukaryote species category (Ereshefsky 1992b, 1998, 2001). Notice that nothing in this paper casts doubt on the existence of less inclusive units than a prokaryote species category or a eukaryote species category. Prokaryote taxa can be divided into recombination units, ecological units, and so on. Eukaryote taxa can be divided into interbreeding units, ecological units, and so on. Such classes of taxa may have explanatory and predictive utility, and thus they may be good candidates for real categories in nature. But such categories are less inclusive than a general species category, a prokaryote species category, and a eukaryote species category.

Going back in time, Darwin looked forward to a future where biologists would not be "incessantly haunted" by the species problem (1859: 494). Darwin, so some argue, was skeptical of the species category but not of those taxa called 'species' by competent naturalists (Beatty 1992; Ereshefsky 2009). His arguments against the species category turned on his doubts over the distinction between species and varieties. This paper cites the heterogeneity of the class of taxa we call 'species' as a reason to doubt the existence of either a prokaryote species category or a general species category for all of life. When it comes to those taxa labeled 'species' by prominent species concepts, we can, like Darwin, remain confident that they exist. They are just not species taxa.

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